THE FLESHY-FRUITED GALIUM SPECIES OF CALIFORNIA (RUBIACEAE).

I. CYTOLOGICAL FINDINGS AND SOME TAXONOMIC CONCLUSIONS

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Preliminary work by the senior author, done under the auspices of the Jepson Herbarium, demonstrated the presence of morphological, cytological and taxonomic complexity in the fleshy-fruited species of *Galium* of California. It was apparent that only by further study of the chromosomes would it be possible to determine the interrelationships between the many existing forms. This study was undertaken in 1963 and 1964, supported by the National Science Foundation, grant number GB649. It has involved an intensive and extensive field investigation, including visits to a number of areas where the plants had not been previously collected. Chromosome counts were made chiefly from somatic cells of leaf buds, either preserved in the field or taken later from transplanted individuals. Material was pretreated with a saturated aqueous solution of paradichlorbenzene before fixing, as a result of which pretreatment the shape of the chromosomes as seen in the figures has been considerably altered.

We wish to thank Rimo Bacigalupi, Curator of the Jepson Herbarium, for generous provision of laboratory space, and for critical reading of the manuscript.

The plants under consideration are dioecious, have four "leaves" to a node (with the exception of *G. hardhamiae* and sometimes *G. clementis*), and bear fleshy fruits, a character unusual in this genus. The species that comprise the group are *G. californicum* H. & A., *G. nuttallii* Gray, *G. bolanderi* Gray (including *G. pubens* Gray), *G. andrewsii* Gray, *G. ambiguum* Wight, *G. sparsiflorum* Wight, *G. miguelense* Greene, *G. muricatum* Wight, *G. clementis* Eastw., *G. grande* McClatch., and *G. hardhamiae* Dempst.

The group is restricted to California, southern Oregon and northern Baja California. Within this area it occupies most of the cismontane hilly and mountainous areas, from ocean bluffs at near sea level to almost 8000 feet in the Sierra Nevada.

Considered from the traditional morphological and geographic points of view, the species have in the past proven difficult to delimit. Many specific names have been published to cover the various forms, and all attempts to evaluate these by classical taxonomic means have been unsatisfactory, owing to the great diversity of forms within what appeared to be the chief divisions or species, and to marginal resemblances be-

tween these species. Preliminary chromosome counts showed the existence of polyploidy, and an attempt has therefore been made by further cytological study to arrive at a clearer understanding of the taxonomic divisions, and eventually of the evolutionary pattern within the group.

The present paper has as its purpose the publication of chromosome numbers (table 1, figs. 1, 2) together with some taxonomic conclusions to be derived therefrom. Our new knowledge of ploidy levels within the group has clarified a number of previously obscure taxonomic lines, such as those between *G. californicum* and *G. nattallii,* and between *G. bolanderi* and *G. sparsiflorum* or *G. nuttallii.* It is hoped, therefore, that a systematic revision based on these new data will shortly follow. Voucher specimens for all chromosome counts will be deposited in the herbarium of the University of California at Berkeley, except those already in the Jepson Herbarium.

The fleshy-fruited *Galium* complex is now known to consist of one widely distributed and polymorphic diploid species, *G. nuttallii,* at least six other more restricted and more uniform diploid species, and at least ten polyploids, most of which are apparently hybrids. All of the diploids can be related readily to one or more polyploids and vice versa, the result being a network of polyploids and diploids in which most, or perhaps all, of the taxa are connected to each other, directly or indirectly.

In the following paragraphs, some specific taxonomic conclusions are set forth, and two new taxa are described.

The epithet *pubens,* derived from *Galium pubens* Gray, the application of which has always been vague and uncertain, is now clearly seen to be unnecessary. Field observation has repeatedly shown us that very pubescent forms referable to *G. pubens* grow in very close association or even in contact with glabrous or glabrate forms of *G. bolanderi,* and that highly diverse populations are common, containing plants of all degrees of pubescence. Since we now know that all of these varying elements of such populations are hexaploid, there seems no good reason to doubt that they are merely genetic segregates in freely interbreeding populations of *G. bolanderi.*

Galium grande McClatch., which has sometimes been confused with *G. pubens* in the herbarium and in the literature, is not only quite distinct in the field, owing to its more fleshy leaves and its lavishly sprawling habit, but is now known to be a very high polyploid, perhaps 20x. It must therefore stand as a species. It was subordinated to *G. pubens* as a variety by Jepson (1925), Munz (1959) and Ferris (1960), and in the latter instance was defined so as to include much pubescent material of *G. bolanderi* from the southern Sierra Nevada.

Galium sparsiflorum Wight is now known to be a diploid species, a fact which greatly eases the matter of differentiating it from some forms of *G. bolanderi.* The latter species is always hexaploid, although some individuals resemble the diploid taxa *G. sparsiflorum* or *G. nuttallii.* The inference is very strong that one genome from each of the latter two

species is present in *G. bolanderi,* together with a third genome from some pubescent species. True *G. sparsiflorum* can be distinguished from sparsifloroid individuals of *G. bolanderi* by the narrow leaf insertion, the very slender pedicels, and often by the leaf texture, which may be thin or somewhat coriaceous, but is never soft and thick as is common with *G. bolanderi.*

Galium muricatum Wight, which was included under *G. californicum* by Jepson but was recognized as a species by Munz and by Ferris, is clearly a separate species. It has been observed repeatedly by us in the field, growing in closest association with *G. californicum* without intergrading. Furthermore, cytological study shows the two species to be far apart in their chromosome numbers, *G. californicum* being, except for the very local ssp. *luciense,* highly polyploid, and *G. muricatum* of low ploidy. The latter is apparently always diploid south of Albion, Mendocino Co., and tetraploid north of Fort Bragg. No consistent difference between the diploid and tetraploid series of populations has yet been found.

Galium cliftonsmithii (Dempster) Dempster & Stebbins, comb. nov. *Galium nuttallii* Gray var. *cliftonsmithii* Dempster, Brittonia 10:183. 1958. Studies since 1958 indicate *G. cliftonsmithii* to be a high polyploid, while *G. nuttallii* is consistently diploid throughout its many forms. The closest relative of *G. cliftonsmithii* is probably *G. californicum,* especially the typical form from the Monterey coast, but the large, shiny, coriaceous and acerose leaves, vigorous habit and higher chromosome number of *G. cliftonsmithii* entitle it to specific rank.

Galium californicum H. & A. ssp. **luciense** Dempster & Stebbins, ssp. nov. Plantae perennes dioicae humiles (usque ad 16 cm), caulibus pluribus e rhizomatibus tenuibus diffusis orientibus, ubique molliter pubescentes pallide virides; folia pusilla, 4–6 (10) mm longa, plana vel leviter revoluta, carnosula, elliptica vel leviter obovata, apicibus inermibus; corollae rotatae, galbinae; ovaria dense pubescentes; fructus albi carnosi; chromosomata 44.

Type. Cone Peak, Monterey Co., California, T. 21 S., R. 4 E., Oct. 12, 1960, at about 4000 feet, *Dempster & Hardham 1403* (JEPS 24912). Named for the Santa Lucia Mountains.

Additional collections Monterey Co.: Cone Peak trail ca. ¾ mile north of roadhead, ca. 4500 feet, *Dempster & Stebbins 3921.* Specimens from the ridge between Mill Creek and Alder Creek, Monterey Co., *Hardham 3785,* with very small stomata, appear to be of this subspecies.

The plants are not conspicuously tufted, the many annual stems arising separately from extensive underground rhizomes, clones often covering many square feet. Apparently of very local distribution, ssp. *luciense* grows in forest duff or gravelly talus in partial shade, with *G. clementis* on Cone Peak, Monterey Co. It was supposedly derived as an allotetraploid from *G. clementis* with some other diploid. It shares with *G. clementis* the distinctive light color and dense, soft long hairs. It is readily distinguished from that species, however, by its habit, which

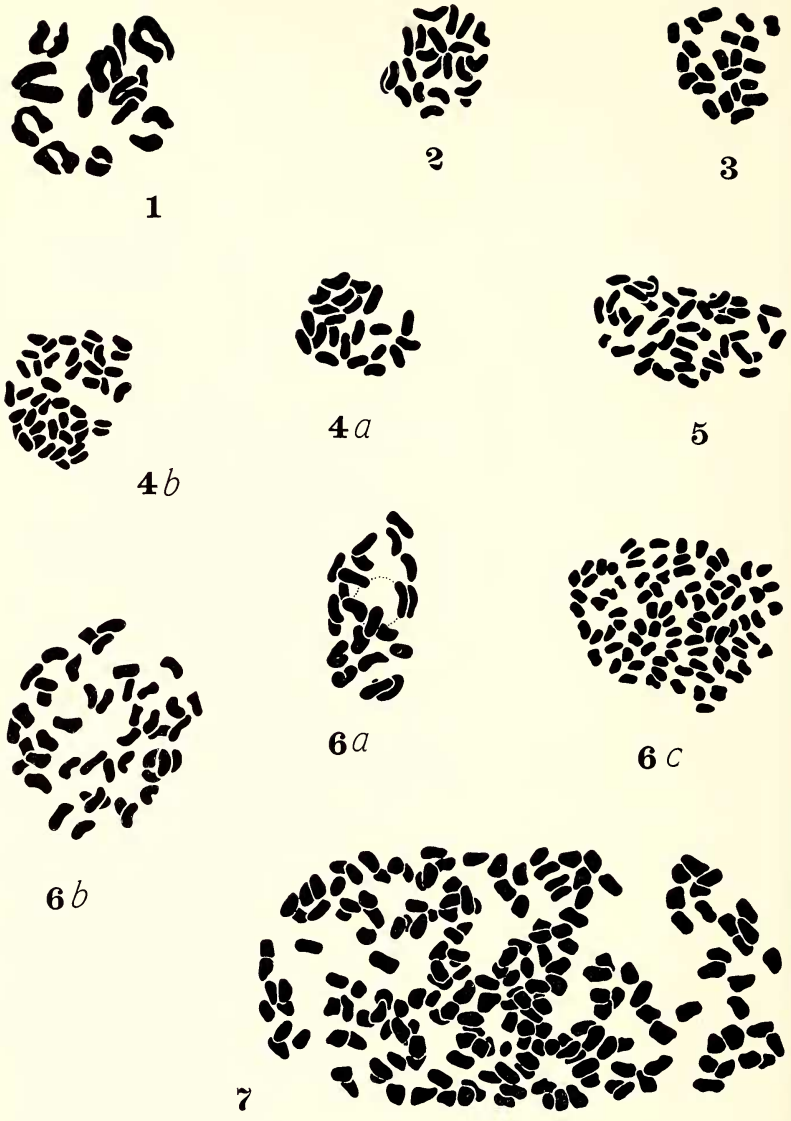
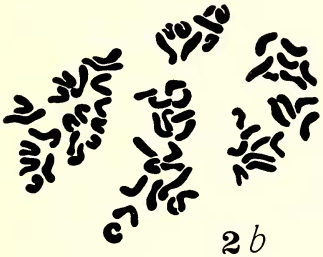


FIG. 1. Camera lucida drawings showing chromosome numbers in species of *Galium* (× ca. 2000). No. 1 is meiotic from P.M.C., the rest mitotic from shoot terminals. 1, *G. sparsiflorum, 3807*, n = 11. 2, *G. clementis, 1402*, 2n = 22. 3, *G. nuttallii, 3968*, 2n = 22. 4a, *G. muricatum, 3944*, 2n = 22; 4b, *G. muricatum, 3957*, 2n = 44. 5, *G. martirense, 3987*, 2n = 44. 6a, *G. andrewsii, 6151*, 2n = 22; 6b, *G. andrewsii, 3983*, 2n = 44; 6c, *G. andrewsii* var. *gatense, 4079*, 2n = 88. 7, *G. cliftonsmithii, 3970*, 2n = ca. 187. All mitotic chromosomes were pretreated with saturated aqueous solution of paradichlorbenzene.

1*a*

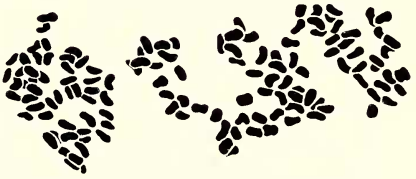
1*b*



2*b*

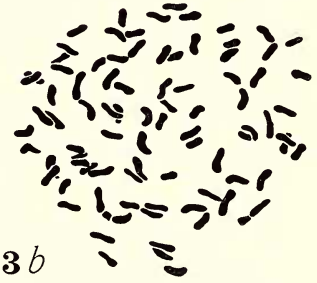
2*a*

3*a*



3*c*

4



3*b*

FIG. 2. Camera lucida drawings showing chromosome numbers of species of *Galium* (× ca. 2000). No. 4 is meiotic from P.M.C., the rest mitotic from shoot terminals. 1a, *G. bolanderi*, *3806*, 2n = 66; 1b, *G. bolanderi* ("*G. pubens*"), *3797*, 2n = 66. 2a, *G. ambiguum*, *4034*, 2n = 22; 2b, *G. ambiguum* var. *siskiyouense*, *3913*, 2n = 66. 3a, *G. californicum* subsp. *luciense*, *3921*, 2n = 44; 3b, *G. californicum*, *3979*, 2n = 88; 3c, *G. californicum*, *3898*, 2n = 132. 4, *G. grande*, *3975*, Anaphase I, 1 pole, n = ca. 110. All mitotic chromosomes were pretreated with saturated aqueous solution of paradichlorbenzene.

is generally lower and much less tufted; by the shape of the leaves, which are considerably broader and not notably revolute; and by the number of leaves, which is invariably four, whereas *G. clementis* often bears five or six to a node. Subspecies *luciense* is, however, less easily distinguished from some forms of octoploid *G. californicum* in the Cone Peak area. Although ssp. *luciense* is relatively uniform in appearance, the octoploid has many forms throughout its range. On the lower slopes of Cone Peak it sometimes resembles ssp. *luciense* rather closely.

On the top of Cone Peak, *G. clementis* is found growing alone. A little lower down, it grows with *G. californicum* ssp. *luciense*. Still lower, *G. clementis* drops out and octoploid *G. californicum* makes its appearance. Lower still ssp. *luciense* drops out, leaving only the octoploid in diverse forms, some very like ssp. *luciense,* a few with narrow leaves suggestive of the deep-shade form of *G. clementis,* but the greater part broad-leaved, flaccid and easily distinguished from both the diploid (*clementis*) and the tetraploid (*luciense*). The new tetraploid taxon may be supposed from its very close morphological resemblance to many forms of *G. californicum* to have been one of the ancestors of that species, and to give us a clue as to the way in which the diploid species *G. clementis* may have contributed to the composition of the modern polymorphic species known as *G. californicum*. It is for this reason, and because of the practical difficulty of differentiating it from some forms of octoploid *G. californicum,* that we have described it as a subspecies of this complex polyploid, rather than as a species.

Galium martirense Dempster & Stebbins, sp. nov. Plantae perennes dioicae 12–50 cm altae, e radicibus robustis caespitosae, caulibus plerumque tenuibus lignosis vix scandentibus, ubique molliter pubescentes pallide virides; folia 5–12 mm longa, apicibus inermibus, plerumque elliptica vel anguste ovata revolutaque, sed nonnumquam latiores vix revoluta; corollae rotatae albo-flavidae extus hispidae; fructus carnosi; chromosomata 44.

Type. Oaks Pasture, 15 miles by crooked road northeast of the Meling Ranch (Rancho San José), about 20 air miles east of San Telmo, Baja California, *Dempster & Cory 3987* (UC 1199709). Named for the San Pedro Mártir Mountains.

Additional collections. Sierra de Juárez: 1 mile south of Rancho Viejo, *Moran 9845* (UC), Ensenada (certainly east of), *Jones 3692* (UC), *Howell* (CAS). Sierra de San Pedro Mártir: northeast of the Meling Ranch (Rancho San José), east of San Telmo, *Dempster 3989* (UC), *3990* (UC), *3991* (UC), *Robertson 12* (UC), *Moran 10950* (UC).

Habitat: Sierra de Juàrez and Sierra de San Pedro Mártir, Baja California, at 3000 to 5600 feet; in shelter of trees, shrubs or boulders, with *Quercus, Adenostoma, Artemisia, Arctostaphylos, Chrysothamnus.*

In growth habit, *G. martirense* somewhat resembles *G. nuttallii,* or even more one of its polyploid derivatives, such as *G. bolanderi,* or coastal forms of *G. californicum*. The primary stems are usually elongated, with nodes sometimes as long as 8 cm, becoming woody but remaining slender and serving as a scaffold for subsequent herbaceous and more congested

fertile growth. The species is most similar to *G. grande* McClatchie, which it resembles more in the herbarium than in the field. Both species are hairy, and often become very dark when dry, the hairs then appearing brownish or white against the blackish chlorenchyma. In habit *G. martirense* is more tufted and the stems are straighter than in *G. grande,* which is decidedly weak and sprawling as well as larger. The leaves of *G. martirense* are generally (although not always) narrower than those of *G. grande* and are noticeably revolute, in contrast with the broader and fleshier, relatively plane leaves of *G. grande*. Nevertheless, a small minority of plants of *G. martirense* with broader leaves and less obviously tufted habit resemble rather closely, at least in the herbarium, a small minority of plants of *G. grande* with narrower leaves or stiffer habit. What at first appears to be a very close relationship is thus not supported by closer inspection, since in addition to the differences in habit and leaves and the wide geographic separation, we find a great difference in chromosome number, *G. martirense* being of low ploidy (4x) as contrasted with the very high ploidy (possibly 20x) of *G. grande*.

Galium martirense seems very closely akin to the diploid species *G. clementis* Eastwood, with which it shares, in most individuals, the narrow, revolute leaves and the pale softly hispid character. *Galium martirense* is, however, a much larger and stiffer plant in every way, with a fair range of morphological variation. *Galium clementis* is apparently restricted in present times to the northern Santa Lucia Mountains in Monterey County, California, and if it was parental to *G. martirense,* it must be supposed that it had formerly a much greater range. If *G. martirense* is an allotetraploid between a *clementis*-like ancestor and some other diploid, the identity of the second ancestor is not apparent. Resemblances to *G. nuttallii* Gray, which in some places grows with it are, except for habit, slight.

Table I. Chromosome Counts in Galium Species of the Fleshy-Fruited Group

Collection numbers are those of Dempster, or Dempster and Stebbins, unless otherwise indicated.

G. nuttallii Gray var. *nuttallii*. **2n = 22.** San Diego Co., Mt. Helix, *3911;* Baja California, Socorro Mine, *Dempster 3991A;* Santa Cruz I., *4085*.

G. nuttallii Gray (other varieties). **2n = 22.** Contra Costa Co., Orinda, *3805*; Humboldt Co., Bull Creek, *3856*, Briceland, *3887*, Shelter Cove, *3888*; Los Angeles Co., Dalton Canyon, *3978*; Madera Co., North Fork, *3813*; Marin Co., Tiburon, *Stebbins s. n.*; Mendocino Co., Albion, *3881,* Anchor Bay, *3948,* Newport *Hutchison 887* (JEPS); Monterey Co., Arroyo Seco Public Camp, *Bacigalupi 7561* (JEPS); Napa Co., Saint Helena, *3780B*, *3780E*; San Benito Co., Clear Creek, *4077*; San Luis Obispo Co., San Luis Obispo, *3960*; Santa Barbara Co., Buellton, *3962,* Nojoqui Falls, *3965,* Refugio Pass, *3968*; Santa Cruz I., *4082, 4088*; Trinity Co., Mill Creek, *3841*; Ventura Co., Ojai, *Dempster s. n.* (JEPS); Josephine Co. Oregon, Merlin, *Hutchison 2065* (JEPS).

G. sparsiflorum Wight. **n = 11.** Fresno Co., Shaver Lake, *3818*; Madera Co., Whiskey Creek, *3807*; Tuolumne Co., Crane Flat, *4035*. **2n = 22.** Placer Co., Baxter, *1443* (JEPS); Tehama Co., Potato Patch, *4050*.

G. hardhamiae Dempst. **2n = 22.** San Luis Obispo Co., Cypress Mountain, *5703* (JEPS).

G. clementis Eastwood. **2n = 22.** Monterey Co., Cone Peak, *1402* (JEPS), *Dempster s. n.*

G. andrewsii Gray. **2n = 22.** Fresno Co., Los Gatos Creek, *4074*, *4075*; Kern Co., Bodfish, *1437* (JEPS); Monterey Co., Castle Peak, *4066*, *4065*, *4069*; Lake Co., Butts Canyon, *Stebbins 6151*; Napa Co., Corona Mine, *Stebbins 6160*; San Benito Co., Clear Creek, *4078*; San Luis Obispo Co., Morro Bay, *Stebbins s. n.*; Tehama Co., west of Paskenta, *3995*, Patton Mills, *3997*, Colyear Springs, *4006*. **2n = 44.** Los Angeles Co., Gorman, *3983*; San Luis Obispo Co., Kiler Canyon, *4073*.

G. andrewsii Gray var. *gatense* Dempst. **2n = 88.** Monterey Co., Parkfield-Coalinga summit, *4072*, Table Mountain, *4064* (D1 & D3); San Benito Co., Clear Creek, *4076*, *4079*, Idria Summit, *4080*; Santa Clara Co., Mt. Hamilton, *4062*.

G. andrewsii x *nuttallii* (natural hybrid). **2n = 22.** Tehama Co., Round Mountain, *4002*.

G. ambiguum Wight. **2n = 22.** Humboldt Co., Low Gap, *3854*; Shasta Co., Harrison Gulch, *4009*, Regan Meadow, *4010*; Tehama Co., Riley Ridge, *4003*, Ball Rock, *4004*, Round Mountain, *4001*; Trinity Co., southeast of Peanut, *4012*, west of Peanut, *4013*, South Fork Mountain, *4022*, Ruth to Zenia, *4026*, Ruth, *4019*.

G. ambiguum Wight var. *siskiyouense* Ferris. **2n = 66.** Del Norte Co., Gasquet, *3912*, *3913*, Happy Camp Road, *3917*.

G. muricatum Wight. **2n = 22.** Humboldt Co., Manchester, *3896*; Mendocino Co., Hendy Redwoods, *3878*, Navarro, *3880*; Sonoma Co., Stewart's Point, *3944*, *3945*. **2n = 44.** Humboldt Co., Willow Creek, *3845* (A & B), Larrabee Valley, *3851*, Dinsmore's, *3852*, Bull Creek, *3858*, Weott, *3860*, Orleans, *3919*, Boise Creek, *3920*, Richardson Grove, *3957* (1 & 2); Mendocino Co., Laytonville, *3871*, Branscomb, *3950* to *3954*, Leggett, *3956* (1 & 3), Willits, *3958*.

G. martirense Dempst. & Stebb. **2n = 44.** Baja California, above Meling Ranch, *3987*.

G. bolanderi Gray (including *G. pubens* Gray). **n = 33.** Butte Co., Jonesville, *4048*; Humboldt Co., Orleans, Hutchison *2031* (JEPS); Madera Co., Oakhurst, *3806* (11 & 12), South Fork, *3809*, *3810*; Placer Co., Baxter, *1442* (JEPS); Napa Co., Angwin, *3782A*; Plumas Co., Quincy, *1458* (JEPS). **2n = 66.** Humboldt Co., Dinsmore's, *3853*, Berry Summit, *Hutchison 2010* (JEPS); Lake Co., Glenbrook Resort, *3797B*; Madera Co., Oakhurst, *3805½*, *3806* (2, 3, 4, 5 & 7), Whiskey Creek, *3808* (1 & 2), South Fork, *3811*, North Fork, *3814*; Mariposa Co., Usona, *3820*; Plumas Co., Graeagle, *1456* (JEPS); Shasta Co., Hat Creek, *4053*; Siskiyou Co., Happy Camp, *3918*, *Hutchison 2039* (JEPS); Trinity Co., Burnt Ranch, *3842*.

G. californicum H. & A. subsp. *luciense* Dempst. & Stebb. **2n = 44.** Monterey Co., Cone Peak, *1403* (JEPS), *3921*.

G. californicum H. & A. sensu lato. **n = 44.** Monterey Co., Kirk Creek, *3939*. **2n = 88.** Los Angeles Co., Glendora Ridge, *3979*; Monterey Co., Cone Peak, *3922* to *3928*, *3933* to *3935*, Nacimiento, *3936*, *3937*; Santa Barbara Co., Nojoqui Falls, *3963*, *3964*, Refugio Pass, *3969*. **2n = ca. 88.** Monterey Co., Cypress Mountain, *1187* (JEPS); Santa Barbara Co., Buellton, *3961*. **n = 66.** Marin Co., Mt. Tamalpais, *Bacigalupi 8880* (JEPS); Trinity Co., Ruth Lake, *4017*. **2n = 132.** Humboldt Co., Manchester *3898*; Mendocino Co., Stewart's Point, *3907*; Monterey Co., Point Lobos, *4081*; Santa Cruz Co., Boulder Creek, *Stebbins s. n.* **2n = ca. 132.** Humboldt Co., Bridgeville, *3848*, Manchester, *3897*; Mendocino Co., Anchor Bay, *3909*, Laytonville, *3872*, *3955*, Bell Springs, *3866*, Hendy Redwoods, *3877*; Santa Cruz Co., Santa Cruz, *Stebbins s. n.*

G. cliftonsmithii (Demps.) Dempst. & Stebb. **2n = c. 182-189.** Santa Barbara Co., Refugio Pass, *3970*.

G. grande McClatchie. **n = more than 110.** Los Angeles Co., Chantry's Flat, *3975*.

Summary

Chromosome counts are published for all mainland species of the fleshy-fruited species of *Galium* of California and environs, showing the complex polyploid nature of the group. Some specific taxonomic conclusions are drawn, and two new taxa are described: *G. californicum* ssp. *luciense* of the Santa Lucia Mountains and *G. martirense* of Baja California. A former variety is raised to specific rank as *G. cliftonsmithii.*

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A FURTHER DESCRIPTION OF GOSSYPIUM TRILOBUM

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The exact nature of the Mexican plant originally described by De Candolle (1824) as *Ingenhouzia triloba* has never been clear, and considerable doubt has been expressed that it is, in fact, distinct from *Thurberia thespesioides* A. Gray. It is now possible to provide a more complete description and on such a basis to resolve the doubt by asserting that these two species are indeed distinct.

De Candolle's generic name was noted by Tidestrom (in Dayton, 1927) as a variant spelling of *Ingenhoussia* Dennst. 1818 and therefore to be illegitimate under Article 64. Irrespective of this rejection, however, it is generally accepted that both De Candolle's and Gray's plants belong in *Gossypium* L.

A third name, *G. lanceiforme* Miers, was subsequently published that is probably based on an isotype of De Candolle's species (Kearney, 1952). A historical summary of the taxonomic disposition of these three names is presented in Fig. 1.

Mauer's publication (1954) of three varietal names under *G. trilobum* contravenes Articles 26 and 36; the varietal names therefore are not validly published.

Gossypium thurberi Tod. (= *Thurberia thespesioides* A. Gray) is a plant, well represented in herbaria and in living collections, that occurs in southern Arizona, northern Sonora, and parts of western Chihuahua. It has been described and illustrated many times, notably among the